The structure and context of male and female song in dippers

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Abstract

Female song in birds is more widespread than previously thought but remains poorly studied. Relatively few researchers have compared the structure and function of female song with that of conspecific males, especially in non-duetting species. Here, we investigate male and female song in the Dipper (*Cinclus cinclus*), a highly territorial and largely monogamous passerine with a complex song in both sexes. The songs of individually marked birds were recorded over a three-year period in order to compare the acoustic structure and production of song in males and females at different stages of the breeding cycle. No differences were found in the complexity, frequency or temporal characteristics of male and female songs. However, unpaired males recorded early in the breeding season sang more complex songs than males that were paired up and nest-building or whose breeding attempts were underway, suggesting that male song is used for mate attraction. By contrast, females sang most often during aggressive encounters with birds from outside their territory. Furthermore, males sang throughout the breeding season when they are highly territorial, whereas females rarely sang after laying had begun. Together, these results support findings from other species that song structure varies with context and suggest that female song in Dippers may be used primarily in mate or territory defence.

Keywords: acoustic structure, birdsong, *Cinclus cinclus*, Dipper, female song, vocal communication

Introduction

The two main functions of song in male birds are mate attraction and territorial defence (Catchpole and Slater, 2008). Song is thought to be an honest signal of male quality because it is costly to produce (Searcy and Yasukawa, 1996; Nowicki, Peters and Podos, 1998; Gil and Gahr, 2002; Catchpole and Slater, 2008). While several studies have shown that song production may not be demanding in terms of metabolic energy consumption (Franz and Goller, 2003; Ward, Lampe and Slater, 2004), singing at a high amplitude or from obvious song posts can increase predation risk (Gil and Gahr, 2002) and time spent singing is time taken away from other activities such as foraging (Oberweger and Goller, 2001). The complexity of male song is widely considered to be a sexually selected trait in many species (Searcy and Andersson, 1986; Catchpole, 1987; Macdougall-Shackleton, 1997; but see Byers and Kroodsma, 2009) and, in some cases, the size of regions of the brain such as the HVC is positively correlated with song complexity and the ability to learn a larger quantity of songs or song components (Nowicki, Searcy and Peters, 2002; Pfaff *et al.*, 2007; but see Gahr, 2007; Hall *et al.*, 2011).

Repertoire size is a measure of the number of either unique songs or syllable types used by an individual (Hiebert, Stoddard and Arcese, 1989; Potvin and Clegg, 2015). In many species, males and females are sensitive to the diversity of syllables within a song, and repertoire size is thought to play an important role in intrasexual selection, mate choice and reproductive stimulation (Searcy and Yasukawa, 1996; Nowicki, Peters and Podos, 1998; Gil and Gahr, 2002). Correlations have been found between repertoire size and a number of individual and life history traits including condition (Kipper *et al.*, 2006), territory size (Buchanan and Catchpole, 1997) and tenure (Hiebert, Stoddard and Arcese, 1989; but see Beecher *et al.*, 2000), parental effort (Buchanan and Catchpole, 2000) and reproductive success (Potvin, Crawford, Macdougall-Shackleton, and MacDougall-Shackleton, 2013). Furthermore, several studies have shown that song complexity (Järvi, 1983; Nelson and Croner, 1991; Ammer and Capp, 1999) and specific acoustic characteristics (Catchpole, 1983; Nagle and Couroux, 2000) can change with motivation, season or age. For instance, it has been shown that migratory and sedentary Blackcap (*Sylvia atricapilla*) populations have different intra- and inter-sexual song characteristics (Collins *et al.*, 2009).

Female song was once thought to be rare but recent work has shown that it is widespread, especially in the tropics and Australasia (Odom *et al.*, 2014; Hall and Langmore, 2017). Most research has focussed on duetting species (Langmore, 1998; Slater and Mann, 2004; Logue and Krupp, 2016) but far less is known about

the function of solo female song in other birds. In some cases there is evidence for a role in territory or resource defence, including monogamous species with year-round territoriality (Brunton and Li, 2006; Price *et al.*, 2008; Tobias *et al.*, 2016) and polygynous species such as the Red-winged Blackbird (*Agelaius phoeniceus*), in which females defend their own sub-territories within a male's territory (Beletsky, 1982). In other cases it may reduce the incidence of polygyny (Langmore, 1998), coordinate breeding activities (Ritchison, 1983) or maintain pair bonds (Hovekamp, 1996). Mate attraction has rarely been reported as the function of female song, although this has been suggested for the polygynandrous Alpine Accentor (*Prunella collaris*; Langmore et al. 1996). However, female song can be easily overlooked in species where individuals only sing for a small window of the breeding season or in monomorphic species where it is difficult to distinguish between the sexes (Langmore, 1998; Hahn, Krysler and Sturdy, 2013; Odom and Benedict, 2018). Moreover, few studies have directly compared the acoustic structure of male and female song, or the behavioural and seasonal contexts in which the two sexes sing. In House Wrens (*Troglodytes aedon*), it has been shown that males use song for mate attraction but both sexes can sing to defend resources or to communicate with their partner (Krieg and Getty, 2016). Such comparisons may offer important insights into the function and evolution of female song in other non-duetting species.

Here, we investigate the structure and potential functions of song in male and female White-Throated Dippers (*Cinclus cinclus*, hereafter 'Dippers'). The Dipper is a sexually monochromatic, riverine songbird that defends linear territories year-round and is one of relatively few passerines of the Northern temperate zone in which both sexes are known to sing regularly (Tyler and Ormerod, 1994; Odom *et al.*, 2014; Odom and Benedict, 2018). Song in Dippers has been reported year-round with the exception of the late summer months when birds undergo a post-breeding moult (Tyler and Ormerod, 1994). High rates of song have been noted particularly during territory settlement and defence, early in the breeding season (Tyler and Ormerod, 1994). The song has been described as "a very sweet rippling warble" with female song "a less sweet series of whistles and disconnected units", but no formal analysis of song has been carried out to date (Cramp and Simmons, 1988; Villain *et al.*, 2017). We recorded and analysed the songs of individually marked birds in a wild population in order to compare: (1) the acoustic structure of male and female song; (2) the acoustic structure of song produced at different stages of the reproductive cycle; and (3) the seasonal patterns in song production for males and females.

Methods

Song recording and spectrogram production

Song was recorded from January to July (2014-2016) in a marked population of 40-50 pairs of Dippers in the River Lune catchment near Sedbergh, Cumbria, UK ($54^{0}323$'N, $2^{0}528$'W). Each year, all unmarked adults are trapped and ringed using mist nets or hand nets placed over the nest; nestlings are ringed when they are nine days old. Every individual is given a unique combination of three plastic colour rings and a standard British Trust for Ornithology metal ring. All individuals were identifiable from their unique combination of colour rings and had been sexed at capture according to their wing length (Andersson and Wester, 1971; Svensson, 1992); for most individuals, sexing could be confirmed from observations of reproductive behaviour (e.g. incubation is carried out by the female only; Tyler & Ormerod 1994) and in no cases was there a discrepancy between the two methods. Each year, all nests within the study population were found and closely monitored to record parental identity, the timing and outcome of reproduction, and a number of behavioural and life history traits. Within this population, some pairs remain together throughout the winter but other individuals start to pair up in January or early February. Nest-building typically begins in late February or March and most clutches are laid in March and April; the female alone incubates the eggs (for 16-17 days) but both parents then provision the offspring throughout the nestling period (21-22 days), with the last nests fledging in June or early July. Dippers are socially monogamous with a low frequency of extrapair paternity (Øigarden, Borge and Lifjeld, 2010), and adults in the study population typically breed for 2-3 years but exceptionally up to 8 years (SPS, unpublished data).

Songs were recorded from distances of 10-15m using a Sennheiser ME66-K6 shotgun microphone with a Rycote Softie windshield and a standard pistol grip connected to a Marantz PMD661 MKII solid state recorder with a sampling frequency of 44.1 kHz; files were stored in WAV format. The site was visited daily throughout the breeding season in 2014 and from January to May in other years, with only a few exceptions due to extreme weather conditions; sampling effort was spread evenly across the field site throughout these periods, with each territory visited at least once per week. Recordings were made opportunistically after May in 2015 and 2016. Upon sighting a given individual, the observer waited 30 minutes; if it did not produce song in that time the observer moved onto the next individual. If a focal individual (male or female) began to sing this was recorded until the bird: (1) disappeared and could not be relocated; (2) changed behaviour, e.g. to foraging; (3) remained

129 silent for 30 minutes; or (4) had been recorded for more than an hour and a large amount of song had been
130 collected. Complete songs were defined as having a minimum of a 0.5 s pause between them. The mean (± SD)
131 pause between syllables was 0.23 ± 0.05 s (range = 0.11-0.33; n = 10 songs from each of 45 individuals). The
132 mean pause between songs was 6.50 ± 3.70 s (range = 0.6-64.0; n = 10 pairs of successive songs from 26
133 individuals).
134
135 **Acoustic structure**
136
137 A minimum of 10 songs was recorded for each of 34 males and 11 females. In order to standardise the
138 number of songs analysed (see below) but maximise the number of individuals included, analyses were
139 restricted to 10 songs per bird. If more songs than this had been recorded for a particular individual, 10 were
140 selected after those with the lowest signal to noise ratio had been excluded. For each individual, all 10 songs
141 were recorded in the same 2-3 week period and birds were categorised according to their breeding stage during
142 this time (see below). A number of complexity, frequency and temporal song characteristics were then measured
143 for each individual and compared between males at different breeding stages, and between males and females
144 recorded at the same stage. These measures were as follows: syllable diversity and versatility (complexity);
145 maximum, minimum and average peak frequency (frequency); and average song length, average syllables per
146 second and song rate (temporal).
147 Syllable repertoire size in Dippers appears to be large. We carried out preliminary analyses of this trait
148 using simple enumeration (Botero *et al*., 2008), but when plotting the cumulative number of unique syllables
149 against the total number of syllables analysed, the curve for only 1 out of 45 individuals reached an asymptote.
150 One individual, for which 22 songs had been recorded and analysed, was found to produce in excess of 157
151 unique syllables with no asymptote reached. Rather than estimating syllable repertoire size, we therefore
152 calculated the number of unique syllables produced in a standardised sample of 10 songs (hereafter, 'syllable
153 diversity'), the minimum number of songs recorded with sufficient quality for analysis. This was considered a
154 biologically meaningful sample as individuals rarely produce more than 10 songs in a single bout, hence most
155 receivers would typically hear fewer songs before responding (LM, unpublished data).
156 Syllable diversity was measured using visual and auditory inspections of spectrograms (Fig. 1),
157 produced using Avisoft SASLab Pro, version 5.2.08 (Specht, 1993), with a 512-point fast Fourier transform
158 length and Hamming window function, 75% frame size, a 87.5% window overlap 86 Hz frequency resolution

and 1.45 ms time resolution. All songs were also high pass filtered at 1 kHz to remove low frequency background noise (e.g. the sound of the river); this threshold was chosen because preliminary analyses revealed that a small number of Dipper songs contained elements as low as 1.03 kHz. First, elements were identified (the smallest continuous tracing on a spectrogram) which were then grouped into syllables where appropriate. Syllables comprised multiple elements, each of which was never produced in isolation; the pause between elements within a syllable was less than 0.1 s and therefore smaller than the minimum pause between syllables. Measurements were first carried out in full by one observer (LM), with each unique syllable being given an identifier. This process was then validated by a second observer (SPS) using a sub-sample of songs and applying the same procedures but without knowing the previous results. Using one full song from each of 10 individuals, 93.9% of all syllables (= 279/297) were catalogued in the same way by both observers and there was no significant difference in the total number of unique syllables per song measured by the two (paired t-test: $t = 1.309$, $df = 9$, $P = 0.223$; 9 measures differed by 1 and the other differed by 2). Versatility was calculated by dividing the number of unique syllables found within one song by the total number of syllables found in that song (Järvi, 1983). This measure was then averaged across each of an individual's 10 songs.

A range of frequency and temporal characteristics were also measured using Luscinia version 2.02.10.15; spectrograms were produced using a fast Fourier transformation with a Gaussian analysis window, 80% spectrogram overlap, 10 kHz max frequency, 5 ms frame duration, 1 ms time step and 2 dB noise removal (Lachlan, 2007). All measurements were based on peak frequency, which is the frequency of maximum intensity (i.e. highest amplitude) for each syllable; this was calculated from 50 measurements taken across every syllable in each song (using the standard settings in Luscinia). The maximum, minimum and average (per syllable) peak frequency (in kHz) were taken for each individual from the total sample of songs. Average song length (in seconds) was calculated across the 10 songs to the nearest 0.05 s; average syllables per second was calculated by dividing the number of syllables found in each song by song length and then averaging over the 10 songs analysed for each individual. Song rate was calculated using the number of complete songs produced within a single 30-minute period of observation for each individual during which the bird sang at least once, starting at the time when the bird was first observed singing.

Breeding stage

For every individual, the breeding stage was classified according to the paired status and reproductive stage of the bird at the time of recording. Three mutually exclusive categories were defined: (1) 'solo' songs were those of individuals recorded in January or February that had yet to be seen with a partner; (2) 'pre-breeding' songs were given by individuals that had been seen with the same partner on at least two occasions foraging, prospecting or nest-building together; and (3) 'breeding' songs were those of individuals which had paired up and had nests at the laying, incubation or nestling stage. The identity of any conspecifics which could be seen by the observer, other than the breeding partner of the singer, was recorded whenever possible. Each individual's 10 songs were recorded during the same breeding stage (the first in which the complete sample size of 10 songs was obtained), so comparisons of songs produced at different stages were not pseudoreplicated (males: n = 10 solo, 14 pre-breeding and 10 breeding; females: n = 2 solo, 8 pre-breeding and 1 breeding). Insufficient recordings were obtained to allow comparisons of the songs produced by the same individual (male or female) at different breeding stages. Statistical comparisons between the sexes were restricted to pre-breeding individuals due to the small sample of females recorded singing at other stages; similarly, statistical comparisons between stages were restricted to males. Solo females are rarely encountered as they are highly mobile (SPS, unpublished data) and only a single breeding female was ever recorded singing.

Female song context and seasonal trends

To further investigate the possible function of female song, all observations over the data collection period were classified according to the behavioural context in which the song was produced: (1) 'aggression' described situations in which a singing female was observed in the presence of at least one conspecific other than her partner and during which antagonistic behaviour (e.g. chasing or fighting) was observed; (2) 'nest-building' was used for songs recorded during the prospecting or nest-building phase of the breeding season which were almost always given in the presence of her mate; and (3) 'other' was used for the small number of songs recorded which could not be classified into either of the other contexts. The use of song in these contexts was then compared over the season by using the context in which each female was first recorded singing in each month; only one female produced song in more than one context per month, and only on a single occasion.

To investigate seasonal variation in song production, the proportion of individuals of each sex which sang at least once during a sampling session was calculated for every day of the 2014 season (mean number of individuals sampled per day = 4.59 ± 2.44). Data from 2015 and 2016 were excluded due to insufficient

coverage during the latter part of the season in those years. All dates were converted to a Julian date (1 = 1st January).

Statistical analysis

To compare the acoustic structure of male and female song, t-tests and Mann-Whitney U tests were carried out for normally and non-normally distributed song characteristics, respectively. The songs of males in different contexts were compared using one-way ANOVAs for parametric data and Kruskal-Wallis tests for non-parametric data, with post-hoc Tukey tests or Dunn tests, respectively. All analyses were carried out in R, version 3.2.2 (R Core Team, 2015). We used the Benjamini–Hochberg false discovery rate procedure to control for multiple testing and provide adjusted P values accordingly (Benjamini and Hochberg, 1995).

Results

Acoustic structure, sex and breeding stage

There was no significant difference between the songs of pre-breeding males and pre-breeding females in any of the complexity, frequency or temporal characteristics measured (Table 1, Fig. 2). However, males singing at different breeding stages used significantly different numbers of unique syllables (Table 2); post-hoc tests showed that solo males had a significantly higher syllable diversity than pre-breeding males ($q = 3.48$, $P = 0.02$) or breeding males ($q = 3.48$, $P = 0.02$; Table 2, Fig. 2a). Furthermore, versatility was significantly lower in songs from breeding males than in those from males at other breeding stages (versus solo males: $q = 3.48$, $P < 0.001$; versus pre-breeding males: $q = 3.48$, $P = 0.01$; Table 2, Fig. 2b).

There was no difference in any of the frequency characteristics or in the average length of male songs produced at different breeding stages (Table 2). The number of syllables per second was higher in the songs of breeding males than in those of males from the other stages (Fig. 2c), and song rate was higher in solo males than pre-breeding or breeding males (Fig. 2d); however, these differences were marginally non-significant after correcting for multiple testing (Table 2).

Female song context and seasonal trends

Female song was frequently recorded during aggressive encounters in the early part of the season (Fig. 3). In the encounters during which all individuals present were identified, the female was singing during an interaction with a lone female on five occasions, a lone male on two occasions and a pair on three occasions. The remaining two observations involved unringed individuals and so their sex was unknown. Some females also sang during the nest-building period and occasionally in other contexts, but song was less frequently recorded later in the season (Fig. 3). This seasonal decline was also apparent from the decrease in the proportion of observed females which were recorded singing as the season progressed (Fig. 4b). The proportion of observed males which were recorded singing also peaked early in the season but remained at a relatively high level throughout (Fig. 4a).

Discussion

No differences were detected in the acoustic structure of songs produced by male and female Dippers. This may be because analyses were restricted to pre-breeding individuals and songs produced during this stage might play a similar role in the two sexes. For example, pre-breeding song may function primarily in territorial defence, which is carried out by both males and females (Tyler and Ormerod, 1994; Logue and Krupp, 2016), or the coordination of breeding activities. Alternatively, there may be sexual differences in song characteristics which were not measured here. Studies of other species have reported a difference between males and females in several acoustic parameters which may facilitate sex discrimination, though such differences are sometimes subtle (Yamaguchi, 1998; Pavlova, Pinxten and Eens, 2005; Geberzahn and Gahr, 2011); our sample sizes were relatively small and further analyses are required, especially of songs at other breeding stages and, ideally, including comparisons of the songs produced by the same individual at different stages.

Solo males were found to use significantly more unique syllables within their songs than males at other breeding stages; they also sang at a higher rate, although this trend was no longer significant after correcting for multiple testing. Breeding males produced songs with significantly lower versatility than those of other males and there was a non-significant tendency for these songs to contain fewer syllables per second, suggesting greater repetition. Variation in song characteristics according to an individual's breeding status has been

reported in several species (Ballentine, Badyaev and Hill, 2003; Hall and Langmore, 2017) and presumably relates to the motivational state of the singer. In Dippers, the differences in complexity and song rate between solo males and breeding males suggest that the former may use song for mate attraction. Singing is thought to be an expensive behaviour, in terms of increased predation risk and reduced foraging time if not metabolic costs (Mougeot and Bretagnolle, 2000; Gil and Gahr, 2002; Franz and Goller, 2003; Ward, Lampe and Slater, 2004), and solo males may compensate for this through the increased probability of securing a mate. Measures of song complexity such as syllable diversity or repertoire size are widely reported as sexually selected traits in other species (Catchpole and Slater, 2008), and a similar role has been suggested for versatility (e.g. Järvi, 1983). Further work on sexual selection in Dipper song should investigate the fitness consequences of variation in complexity but might also focus on performance-based song traits, such as consistency, which are thought to be important in some species (Podos, 1997; Botero *et al.*, 2010; but see Kroodsma, 2017).

Observations of females singing were most frequent during the start of the breeding season when territory boundaries are being established between neighbours. Most female song was recorded during aggressive encounters, usually involving another female, during which song presumably functions in defence, either of a territory or a mate. Members of a pair may only defend against same-sex intruders, which would increase the efficiency of defence (Langmore, 1998). This behaviour has been observed in Northern Cardinals (*Cardinalis cardinalis*), in which female song was shown not to deter intrusions by new males but was thought to deter other females (McElroy and Ritchison, 1996). In our study, female song was also recorded during nest-building when the male was present and may play a role in pair-bonding or the coordination of breeding activities, as has been shown in Black-headed Grosbeaks (*Pheucticus melanocephalus;* Ritchison, 1983). Finally, on three occasions females were recorded singing when neither aggressive interactions nor nest-building were taking place. In two cases, the same female was observed singing in the presence of a male who was not her partner; this was at a time when egg-laying was imminent and it is possible that she may have attempted to advertise her fertility to increase chances of extra-pair copulation (Baptista *et al.*, 1993). Another female was observed singing in May whilst accompanied by her partner and when their chicks were a few days from fledging; this female may have been using song to advertise her fertility in preparation for a second clutch (Baptista *et al.*, 1993). Only twelve solo females were observed throughout the entire study, eight of which were recorded singing (two with sufficient regularity to be included in our sample). While our results suggest that mate attraction may not be the primary function of female song, it may be that solo females do sing to attract males but are rarely encountered.

The seasonal decline in the production of song by females is likely due to the energetic constraints imposed by parental care, particularly during incubation and brooding (Brunton, Evans, Cope, and Ji, 2008). Singing on or near the nest may also compromise offspring survival by making nests more conspicuous to predators (Kleindorfer, Evans and Mahr, 2016). In contrast, male song was recorded regularly throughout the breeding season which is in keeping with a role in territorial defence and mate guarding. Our fieldwork ended shortly after each breeding season, and future research on singing behaviour in the second half of the year may shed further light on the different contexts in which both males and females sing.

Finally, it is worth noting that the average peak frequency used by both sexes is similar to that reported for calls in this species, which are concentrated within a narrow frequency range of 4-6.5 kHz (Tyler and Ormerod, 1994). This is likely to enable communication over long distances given the low frequency background noise of their riverine environment (Tyler and Ormerod, 1994), and it has also been reported that individuals sing more frequently in the quieter parts of their territory (Magoolagan, 2012). Even so, the complexity of song has the potential to be masked by the noise of running water and it may be that the frequent visual signals given by dippers, such as dipping, wing flashing and blinking, play a role in increasing perception of song characteristics (Tyler and Ormerod, 1994; Johnstone, 1996).

In conclusion, our study provides one of relatively few direct comparisons of the acoustic structure and seasonality of male and female song in a non-duetting species, together with evidence of context-specific song characteristics in males. The results support previous findings that song structure can vary within a species according to the breeding status of the singer. The observed differences in seasonality between the sexes may simply reflect the energetic constraints of breeding in females, but may also arise from differences in song function between males and females. While no structural differences were detected, sample sizes were relatively small and comparisons were restricted to the pre-breeding stage; further analyses including playback experiments are required to better understand functionality. Furthermore, it is still unknown whether song is a sexually selected trait in female birds (Pavlova, Pinxten and Eens, 2005), and recent findings that female song was likely present in the early ancestors of songbirds raise the question of why this trait has since been lost in some species (Odom *et al.*, 2014; Hall and Langmore, 2017; Odom and Benedict, 2018). Analyses of the relationship between song complexity and fitness would shed further light on the function and evolution of female song in Dippers.

Data availability

The datasets analysed during the current study available from the corresponding author on reasonable request.

Compliance with ethical standards

All procedures performed were in accordance with the ethical standards of Lancaster University. The trapping and ringing of birds was licensed by the British Trust for Ornithology.

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Figure Captions

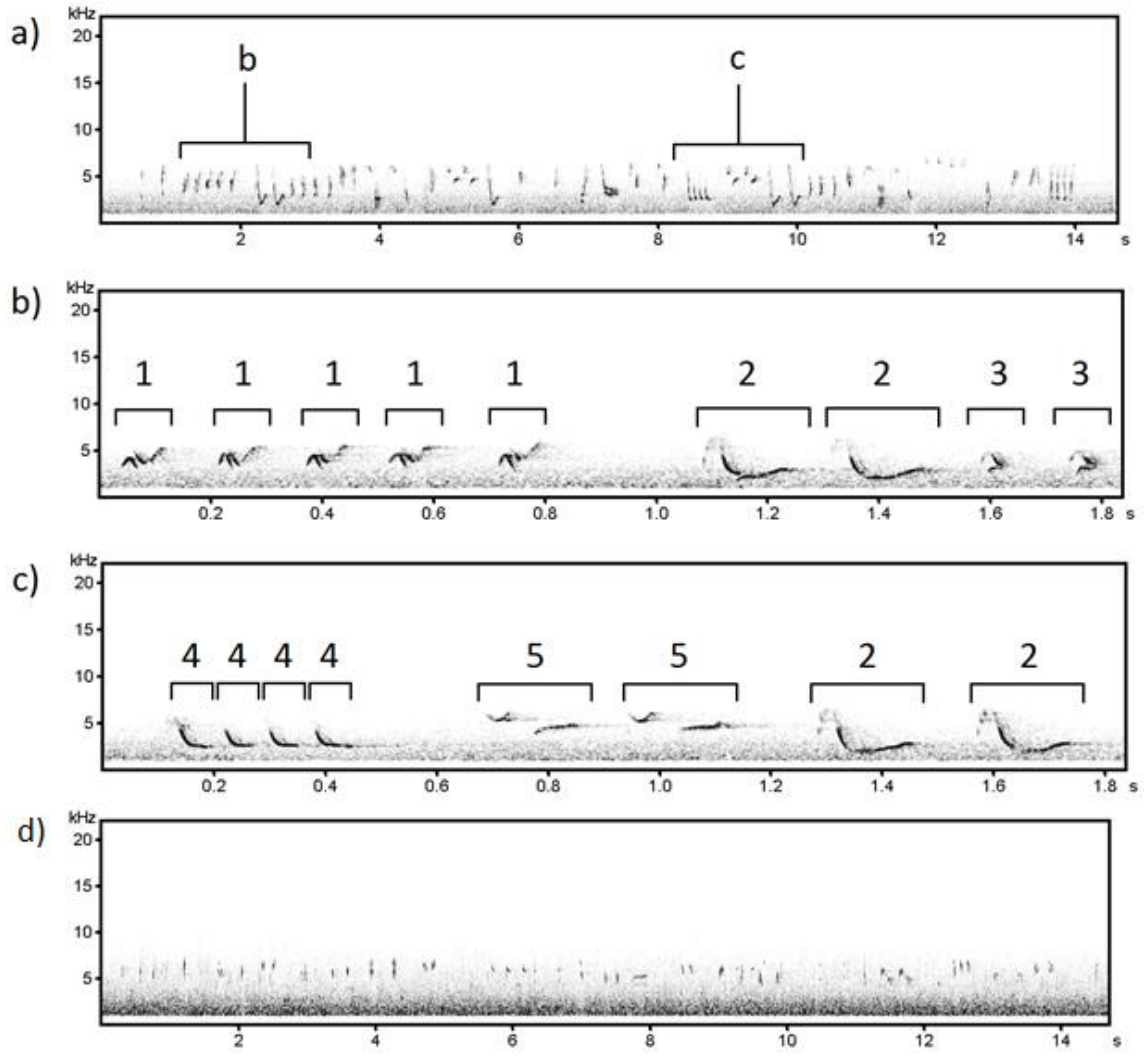
Fig. 1. Spectrograms of male Dipper song: a) full song; followed by sections of that song b) and c), which represent the resolution at which songs were analysed (Avisoft settings as stated in methods). Syllables are numbered, 1 and 5 showing how elements are grouped together to form syllables. Syllables can be repeated straight away (e.g. 1) or appear later in the same song (e.g. 2). A spectrogram of female dipper song (d) is also included for comparison.

Fig. 2. A comparison of song characteristics in male and female Dippers at different breeding stages: a) syllable diversity, b) versatility, c) average syllables per second and d) song rate. Boxes show the median, first and third quartiles; upper and lower whiskers extend to the highest and lowest values that are within 1.5 * the inter-quartile range. Data beyond the end of the whiskers are outliers and plotted as individual points. Syllable diversity is the number of unique syllables produced in a standardised sample of 10 songs. Versatility was calculated by dividing the number of unique syllables found within one song by the total number of syllables found in that song, then averaging across each of an individual's 10 songs. Average syllables per second was calculated by dividing the number of syllables found in each song by song length and then averaging over the 10 songs. Song rate was calculated using the number of complete songs produced within a single 30-minute period of observation for each individual during which the bird sang at least once, starting at the time when the bird was first observed singing. Sample sizes for each sex at each breeding stage are as follows: solo males (n = 10), pre-breeding males (n = 14), breeding males (n = 10), solo females (n = 2), pre-breeding females (n = 8) and breeding females (n = 1).

Fig. 3. The number of observations of female Dippers singing in different behavioural contexts during each month of the breeding season. Within each month, observations correspond to different females because only the first context in which a given female produced song is shown: "aggression" (black) describes females within their own territory which sang in the presence of an intruder i.e. not their partner; "nest-building" (grey) describes females recorded singing whilst prospecting or building a nest with their partner; and "other" (white) describes females which sang in all other contexts.

Fig. 4. The proportion of observed individuals recorded singing for each month of the breeding season for male and female Dippers. Proportions were calculated across all observed individuals per month according to whether

533 or not they were recorded singing at least once in that month. Sample sizes are denoted above the bars for each
534 sex in every month.



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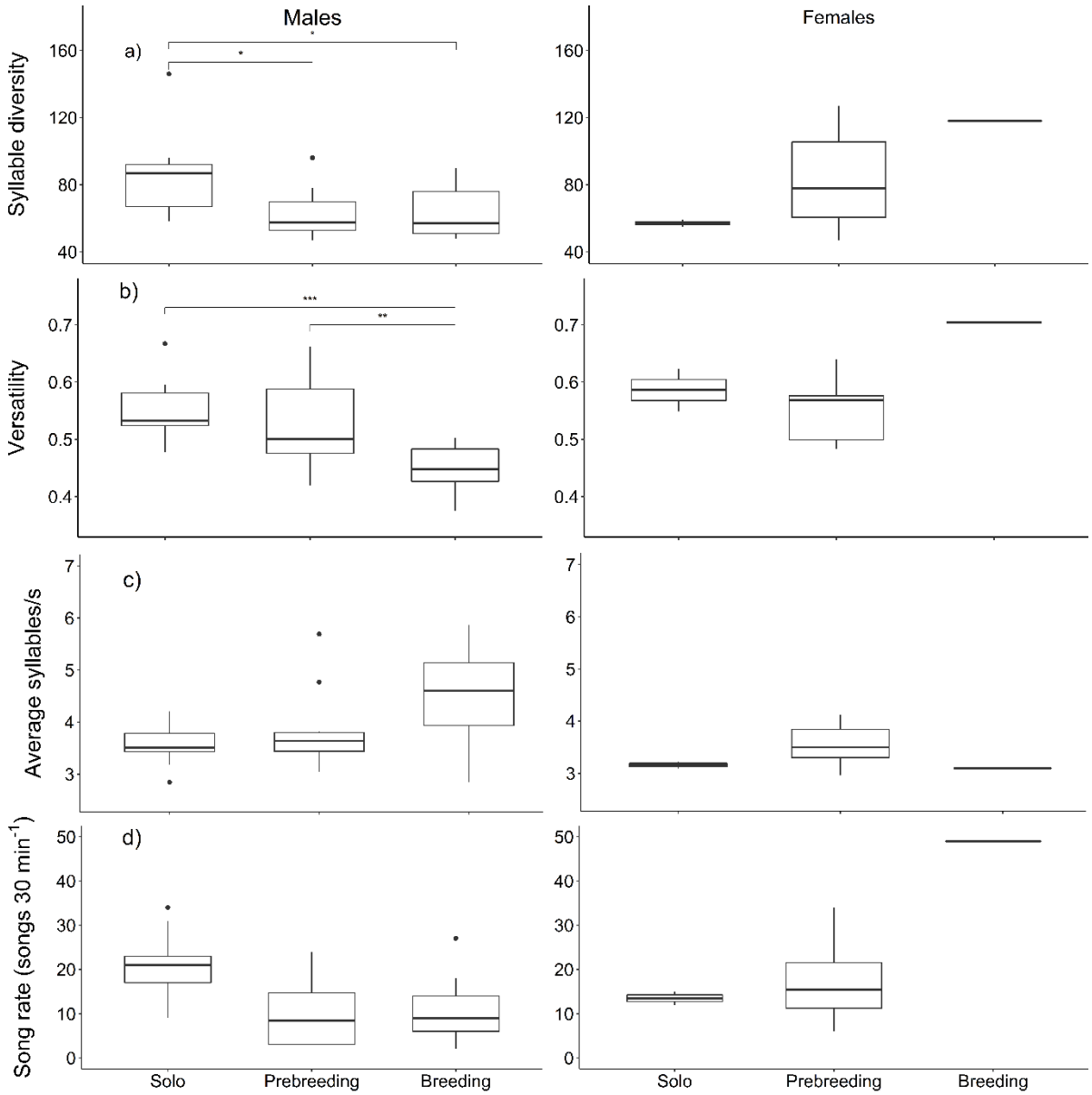

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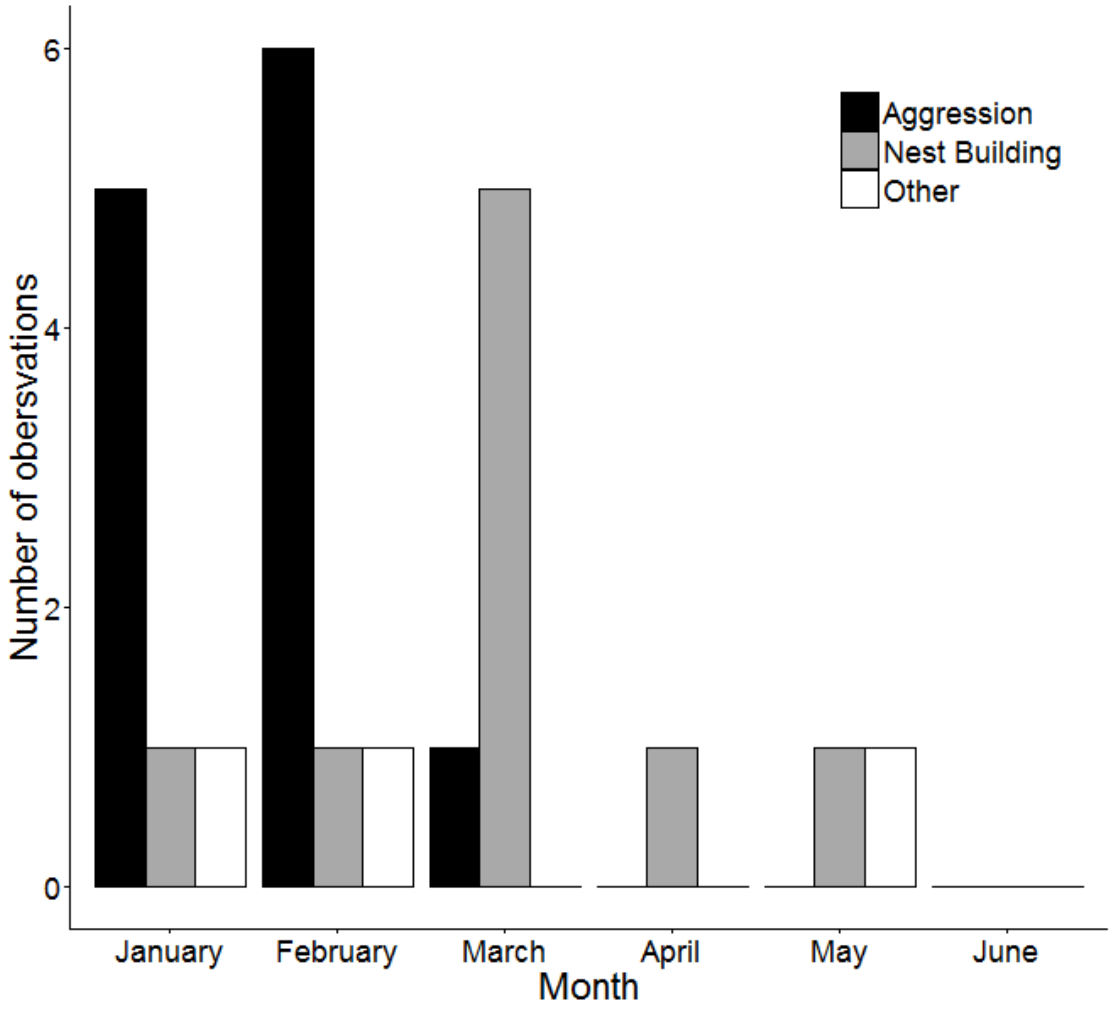

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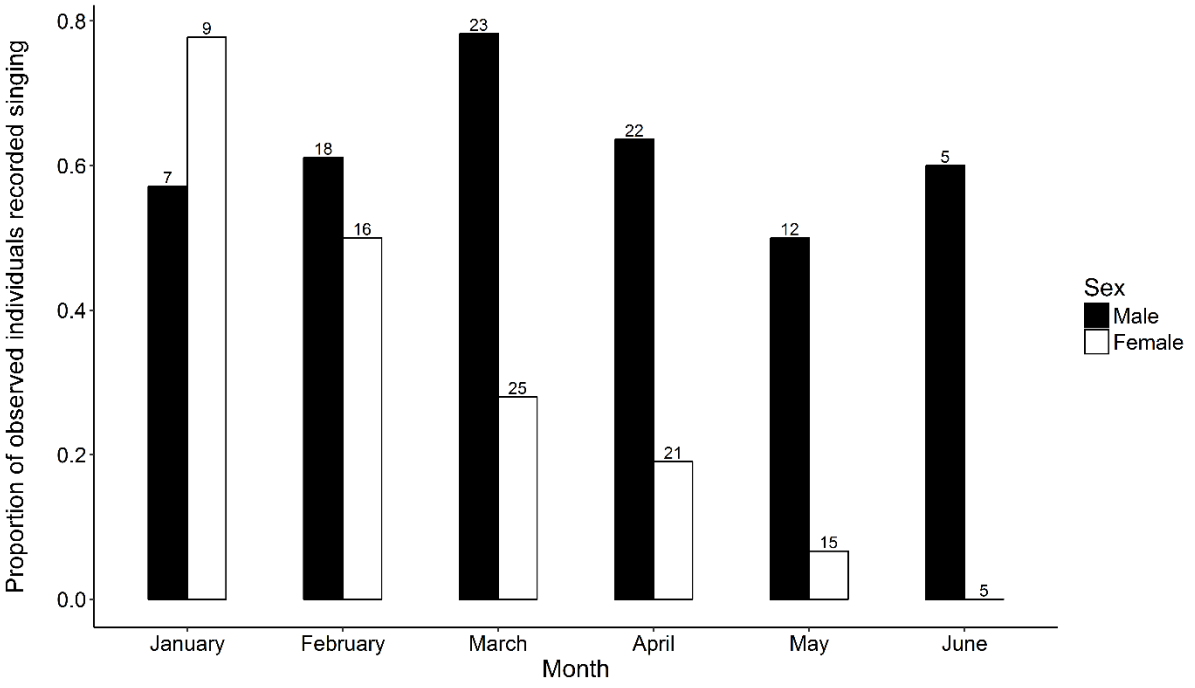

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Table 1. A comparison of the means (± SD) of a range of complexity, frequency and temporal characteristics of song in male (N = 14) and female (N = 8) Dippers. Data are for individuals recorded in the 'pre-breeding' stage only.

Measure	Male	Female	Test statistic (t or W)	p
Syllable diversity	61.5 ± 15.7	82.5 ± 29.3	t = -1.88	0.091
Versatility	0.52 ± 0.07	0.55 ± 0.054	t = -0.90	0.379
Maximum peak frequency (kHz)	8.08 ± 0.52	7.85 ± 0.28	W = 47.5	0.585
Minimum peak frequency (kHz)	1.59 ± 0.36	1.54 ± 0.46	t = -0.26	0.797
Average peak frequency (kHz)	4.91 ± 0.19	4.93 ± 0.19	t = 0.21	0.836
Average song length (s)	6.39 ± 1.79	8.02 ± 3.87	W = 47.0	0.570
Average syllables per second	3.77 ± 0.69	3.53 ± 0.43	W = 64.5	0.585
Song rate (songs 30 min^{-1})	9.79 ± 7.02	16.8 ± 9.32	W = 30.5	0.092

Syllable diversity is the number of unique syllables produced in a standardised sample of 10 songs. Versatility was calculated by dividing the number of unique syllables found within one song by the total number of syllables found in that song, then averaging across each of an individual's 10 songs. Average syllables per second was calculated by dividing the number of syllables found in each song by song length and then averaging over the 10 songs. Song rate was calculated using the number of complete songs produced within a single 30-minute period of observation for each individual during which the bird sang at least once, starting at the time when the bird was first observed singing.

Table 2. A comparison of the means (± SD) of a range of complexity, frequency and temporal characteristics of songs produced by male Dippers at different breeding stages. Sample sizes are given in parentheses; significant differences ($p < 0.05$) are shown in bold. P values are provided before and after adjustment using the Benjamini–Hochberg false discovery rate procedure to control for multiple testing.

Measure	Male songs			Test Statistic	p	p adjusted
	Solo (10)	Pre-breeding (14)	Breeding (10)			
Syllable diversity	85.4 ± 25.1	61.5 ± 15.7	61.2 ± 17.8	F = 5.40	**0.010**	**0.039**
Versatility	0.55 ± 0.053	0.52 ± 0.07	0.45 ± 0.05	F = 8.38	**0.001**	**0.010**
Maximum peak frequency (kHz)	8.42 ± 0.68	8.08 ± 0.52	8.01 ± 0.49	$\chi^2 = 2.13$	0.346	0.461
Minimum peak frequency (kHz)	1.52 ± 0.50	1.59 ± 0.36	1.40 ± 0.42	F = 0.60	0.553	0.553
Average peak frequency (kHz)	4.89 ± 0.42	4.91 ± 0.19	4.75 ± 0.30	F = 0.85	0.438	0.500
Average song length (s)	8.33 ± 3.00	6.39 ± 1.79	6.08 ± 2.10	$\chi^2 = 4.44$	0.106	0.168
Average syllables/s	3.51 ± 0.37	3.77 ± 0.69	4.50 ± 0.93	$\chi^2 = 6.84$	**0.033**	0.066
Song rate (songs 30 min^{-1})	19.4 ± 9.05	9.79 ± 7.02	10.7 ± 7.57	$\chi^2 = 7.32$	**0.026**	0.066

Syllable diversity is the number of unique syllables produced in a standardised sample of 10 songs. Versatility was calculated by dividing the number of unique syllables found within one song by the total number of syllables found in that song, then averaging across each of an individual's 10 songs. Average syllables per second was calculated by dividing the number of syllables found in each song by song length and then averaging over the 10 songs. Song rate was calculated using the number of complete songs produced within a single 30-minute period of observation for each individual during which the bird sang at least once, starting at the time when the bird was first observed singing.